

PROPHYLLS AND BRANCHING IN CYPERACEAE

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Introduction

The prophylls of Cyperaceae have been discussed in a full paper by Blaser (1944), and others, particularly Holtum (1948), Koyama (1961) and Kern (1962), have considered them in relation to spikelet structure and phylogeny. But they do not usually figure in taxonomic descriptions or drawings and are still relatively little known, particularly as regards their distribution in the whole plant.

Here a few Nigerian species growing in the forest zone near Lagos, supplemented by a few plants from elsewhere, are used to illustrate their range of development and their bearing on the evolution of the family. Most of these species are also found in East Africa. The proper identification of the prophylls and the branch systems associated with them underlies many problems of morphology and classification.

In dicotyledons the prophyll or prophylls are taken to be the first leaf or leaves of the shoot, which may be modified in various ways but usually grade into the foliage leaves. In monocotyledons a particular form of prophyll is often found at the base of the shoot, never more than one, always placed dorsally, that is between the shoot and its parent axis, and usually having two more or less equally developed main vascular bundles each with its own keel rather than the single main bundle and single keel of the foliage leaves. It is this unique organ, well developed in Cyperaceae, that is considered in this paper.

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Tubular Prophylls

Fimbristylis obtusifolia (Lam.) Kunth (fig. 1, B-E) is a common tufted perennial of open trodden ground near ponds and lagoons. The foliage

leaves are all basal, but some ensheath the lower part of the rounded culm (B and C). New branches spring as buds from the axis of the leaves, the three branches *a*, *b* and *c* of the fragment shown from the leaves, 3, 4 and 7 of the parent stem. At its base each branch is surrounded by a tubular prophyll, *a*^p, *b*^p and *c*^p. The prophyll carries a pair of ciliate keels ending in short points, and these keels embrace the parent axis (D). As the shoot expands the prophyll is often split to the base on the abaxial side (E). The prophyll is followed by a variable number of foliage leaves arranged spirally, and these, at the culm apex, by the bracts that subtend the branches of the inflorescence.

Fimbristylis obtusifolia has a condensed inflorescence not suitable for analysis, but in *F. dichotoma* (L.) Vahl, a common weed, usually annual, of gassy places, banks and fields, the parts are well spread (fig 1, A and F-L). The lowest bract (F-H, *b*) is longer and set more vertically than the others, and subtends the longest and most complex branch (I), while the succeeding bracts, set, as in most Cyperaceae, at near limit divergence (Hirmer, 1931), decrease regularly in size and bear less complex branches. Each branch is surrounded at its base by a tubular, two-keeled prophyll (I,J) similar to, but much smaller than those at the bases of the culms. The lower branches (1 and 2) are themselves further branched, the upper not so. Each branch ends in a terminal spikelet with the secondary branches, if any, springing immediately below (K,L). The glumes of the terminal spikelet follow the spiral of the bracts without interruption (H,L). One spikelet is terminal to the culm itself and is sessile amongst the major branches (A and G, *t*), and so lies near the base of the whole inflorescence.

In *Fimbristylis dichotoma* the branching at the base resembles that in *F. obtusifolia*, but the lower leaves are reduced to short-bladed sheaths. The leaves have a sub-distichous arrangement, so that the branching comes to be largely in one plane (fig. 2, F and G). In the fragment analysed the leaves *a*⁴ and *a*⁵ of the oldest shoot subtend shoots *b* and *f*, while *a*² has the prophyll of an undeveloped shoot *e*^p hidden in its axil. The shoot *c* is subtended by the leaf *b*² and *d* by *c*² in succession so that all the prophylls of this side of the fragment face towards *a*. But on the other side the shoot *g* is subtended by *f*³ and its prophyll faces the other way, spoiling the symmetry.

Within the spikelet glumes there are no prophylls; nothing corresponding to the paleas of Gramineae. Since every shoot of the plant, from the largest culm axis to the smallest branch, carries a prophyll at its base and a spikelet at its apex, the numbers of prophylls and spikelets over the plant as a whole are, in principle, equal. But while the spikelet of a minor branch lies near its prophyll and its glumes follow the prophyll immediately (fig. 1, K, L), the terminal spikelet of the inflorescence is

separated from its prophyll by the whole length of the culm, and there are many foliage leaves and inflorescence bracts between.

In *Eleocharis mutata* Roem. & Schultes (fig. 2, H, I) the culm ends without branching in a single spikelet, so that there are normally no prophylls except at the culm bases, where they are constant. In the normal spikelet there are no prophylls, nor are they found at any stage of development (Mora, 1960, *Eleocharis palustris* R. Br.). But in proliferating spikelets of *Eleocharis*, sect. *Multicaules* where the florets are replaced by vegetative shoots, Koyama (1961) found them, the only clearly recorded examples of intraspicular prophylls in Cyperaceae.

The *Fimbristylis* species discussed seem, so far as their branch-systems and prophylls are concerned, fair samples of unspecialized Scirpeae. It is generally agreed that the presence of perianth bristles and the relatively simple insertion of the floret in *Scirpus* are more primitive characters than the absence of bristles and winged rachilla of *Fimbristylis* (Koyama, 1961). The branch structure in *S. sylvaticus* L., picked by Monoyer (1934) as the nearest approach in living material to a primitive *Scirpus*, is similar to that in *Fimbristylis*. In *S. pedicellatus* Fernald Blaser (1944), found a gradual transition from a large two-keeled many-veined prophyll of the lowest ray of the umbel to the smallest type which was hyaline and usually without keels or veins. Blaser also noted that in the species of *Scirpus* he examined the prophyll never subtended an axillary bud. A fragment of *S. brachyceras* Hochst. (fig. 2, J), however, shows one prophyll (a) at the base of the branch, and others (b, c) at the bases of the latest spikelets. In the axil of a is an undeveloped spikelet, with its own prophyll (d), and similarly placed spikelets may become fully developed.

Prophyll branching at the plant base

Fimbristylis hispidula (Vahl) Kunth is a tufted, hairy, fast growing annual of dry disturbed places (fig. 2, A-E). The leaves are relatively reduced, the culms serving as the main assimilating organs. The inflorescence is usually less complex than in *F. dichotoma* and is often without secondary branching, as in the head figured by Nelmes and Baldwin (1952), but is of the same structure, with tubular prophylls (E).

At the base of the plant the prophylls are closely packed and conspicuous, and most of the new shoots spring from their axils. A prophyll subtends one shoot, and the prophyll of this shoot the next, without waiting for the parent shoot to mature, a process which leads to a mass of shoots and prophylls facing in different ways (B, C). The young prophylls are conical with only a narrow opening (D) but become split as the shoot expands. Such basal prophyll branching is uncommon but in *Eleocharis*

acicularis (L.) Roem. & Schultes, and *E. palustris* (L.) R. Br. tuft formation in the season following establishment of a new plant depends on this mechanism (Tutin, 1954; Mora, 1960).

Prophyll branching in the inflorescence

Fuirena umbellata Rottb. (fig. 3, A-O) is a soft-stemmed upright plant of wet places and streamsides, often, at least at flood time, partly submerged. The rhizome is creeping, made up of the horizontal bases of successive shoots. The stem is eventually ascending with the leaves spaced along it, the lower reduced to sheaths, the upper foliaceous. The spikelets are set in clusters of about six, arranged in an elongate inflorescence. New shoots break through the bases of the old scale leaves (B), protected at first by short conical prophylls which are split as the shoots expand (C, D), and soon wither. Usually only one such shoot develops from each old stem, but several buds are formed, and these may develop to give a branching rhizome.

The leaves below the inflorescence subtend no branches, nor can any trace of buds be found in their axils. But in the flower bearing region two branches, a major and a minor, appear at the ligule margin of each of the larger bracts (E and F, *mj*, *mn*). Traced to their origins at the bract attachment the two branches are found enclosed together in a delicate tubular prophyll (G), and the minor branch has, besides, its own prophyll (H), arranged as shown in the plan (I). Thus the minor branch springs from the axil of the prophyll of the major branch.

Tubular prophylls similar to those of *Fimbristylis* also surround the smaller branches of the inflorescence (J). But in *Fuirena* the individual spikelets are sessile in the cluster, and their prophylls are shortened so as to be wider than long (K). Further each prophyll bears on its adaxial surface a pulvinus which swells as the inflorescence reaches maturity so as to force each branch or spikelet away from the axis that carries it. At maturity the prophyll persists at the base of the spikelet rachilla while the glumes and nutlets fall from it (L).

Here again the numbers of prophylls and spikelets correspond. The scheme (M) represents the spikelets carried at a single node. The major and minor branches each have a prophyll at the base and end in a terminal spikelet (*t*) which occupies the centre of a cluster and has no prophyll at its base. The other spikelets are arranged in spiral order, each subtended by a bract and each bearing a prophyll at its base. The distinction between bracts, prophylls and glumes is clear. Occasionally, as in the axil of the bract *b*⁴, a spikelet (*in*) may spring from the prophyll of another spikelet. Another example, this time aborted, is seen at the base of the fruiting

spikelet (L, in), with its own prophyll. But whereas prophyll branching is an important feature of the main branch system of the inflorescence, it is relatively rare in the spikelet clusters.

Owing to the elongation of the internodes of the main stem the terminal spikelet of the inflorescence lies near its apex (E, t). It does not usually lie quite at the apex, for the uppermost part of the main stem is deflected and a secondary branch continues its direction.

The floret in this species has three perianth scales, of which the largest lies between the ovary and the rachilla of the spikelet (N, O), so in the position of a prophyll. But it is not two-keeled, and its texture and veining agree with those of the two smaller scales. Further all three scales end in a weak, flexuous bristle, suggesting that the wide basal part of the scale is an expansion of a bristle such as is found in many Scirpeae (fig. 2, I) and, in species of *Fuirena* with six perianth members, in the outer three.

Nees Van Essenbach (1835) believed that the three scales of *Fuirena* were attached within the three stamens and Kern (1962) was also 'pretty sure' that the scales were inside the whorl of stamens. If this were indeed the case the scales could not belong to a perianth and would presumably be bracts. So Mattfeld (1938) and Kern (1962) took each separate stamen in *Fuirena* as a unisexual flower subtended by a bristle, and the ovary as a terminal female flower, the whole bisexual structure being a composite 'synanthium'. They accepted the implication that the florets of other Scirpeae must, since their structure was rather similar, also be synanthia.

But though the filaments of the stamens lie outside the scales both Blaser's (1941, a) beautiful sections and my dissections of fresh material (fig. 3, N) show their attachments at most on a level with the perianth segments and not outside them. There is then no need to consider these florets as synanthia. It seems probable that the many peculiarities of *Fuirena umbellata*, its various types of prophyll with and without a pulvinus, prophyll branching, hollow 5-angled stems and leaf with ligule and adjutor tissue, are, together with the scaly perianth, all specializations. It is more difficult to decide whether the long internode of the culm and shorter internodes of the inflorescence in *Fimbristylis*, or the more uniformly expanded internodes giving the leafy stem and elongated inflorescence of *Fuirena* are the more primitive, or whether both are derived from yet another arrangement.

Dulichium has also been interpreted by Mattfeld (1938), Schultze-Motel (1959) and Kern (1962), as having synanthial florets. Of the 8 bristles the 5 abaxial are inserted below the stamens but the 3 abaxial above. Each group of bristles was interpreted by Mattfeld as the surviving veins of a dissected bract, but Blaser (1944) found the anatomy

of the floret to be of normal scirpoid type, except that the inner bristles were a little displaced, presumably by pressure in the bud. Kern pointed out that neither of the two groups of bristles could be a reduced prophyll as in Cyperaceae the prophylls have no midveins, but still believed that the bristles were reduced bracts, not perianth segments.

In fact Blaser's (1944) figures of prophylls at the base of a major branch and of a spikelet, taken together with Schultze-Motel's (1959) figures of the lowest floret of a spikelet which includes the prophyll (unlabelled) at the spikelet base, show *Dulichium* to be, in general structure, of ordinary scirpoid type. Koyama (1961) has removed it from Cyperae to Scirpeae in spite of the distichous glumes, which may be found in other Scirpeae such as *Scirpus roylei* (Nees) A. A. Beetle and several species of *Fimbristylis* and *Bulbostylis*. Indeed this and other characters such as the cylindrical hollow stems, the evenly spaced equal inflorescence branches, and the shift of the inner bristle suggest a peculiarly specialised type, rather than a relatively primitive form, 'combining characters of Scirpeae, Cyperae and Rhynchosporae', as suggested by Mattfeld. A new study of the plant as a whole is needed.

Serial branching

Though *Fuirena umbellata* usually grows in swamps, it is sometimes found in open places which dry out each year for several months. In this case the rhizomes are straight, with only occasional branches, and are studded with closely packed, hard, black 'bulbs' (fig. 3 P,Q), which sprout at a favourable opportunity. The 'bulbs' lie alternately to the left and right of the sympodial rhizome, and the leaves are set in alternate right and left-handed spirals (arrows in R). Successive branching from the second leaves, f^2 , g^2 , h^2 , etc. gives the straight rhizome with two scales, the first and second leaves of the succeeding culm, between each pair of 'bulbs'. These two scales are intact only in the last shoot j . In the others they are split as the succeeding shoot develops. The third leaf of each shoot makes the outer covering of its 'bulb'. Such 'serial' growth is rare in Scirpeae, but is found in many Cyperae, always dependant on budding from the axil of the second leaf. Buds may be found in the axils of other leaves, as h^4 , giving branching rhizomes.

Prophylls in Cyperae

Cyperus tenuis Swartz (fig. 4, A-H) is common tufted weed of grassy clearings and pathsides in dry, disturbed bush, usually dying off in the dry season. The base of the culm is swollen (B) and carries a variable number of scale and foliage leaves. The lower leaves are split (C) so that it is

difficult to place them, but when they are torn off their positions become clear from the arrangement of the buds developed in their axils. The strictly $\frac{1}{2}$ phyllotaxy, found in all Cyperaceae with sharply triquetrous culms, is attested by three vertical series of buds, each protected by a conical prophyll (B). The tristichy is derived from a distichy in the seedling (Hirmer, 1931).

The primary and secondary umbel branches have tubular, two-keeled bifid prophylls (D,E), resembling those of a *Fimbristylis*. But at the attachment of the prophyll, and probably a part of the prophyll, is a pulvinus which adjusts the position of both the branch and the umbel bract that subtends it. This action is fully discussed by Mora (1960) for *Cyperus papyrus* L., where each of the larger bracts subtends many branches set side by side like a hand of bananas, each branch with its own prophyll. In *Fimbristylis* some of the spikelets are solitary, others grouped into small clusters. This is a common arrangement in other general of Scirpeae, but in some, such as *Holoschoenus*, all the spikelets are grouped. In *Cyperus* the unit is a group, most of the groups carried in the secondary umbels, but some solitary on the shorter branches and one terminal to the culm.

In the group one spikelet is terminal, the rest lateral (F,G). Each lateral spikelet has two empty scales at its base, one the subtending bract (b), the other the prophyll (p), followed immediately by the fertile glumes. The prophyll is scale-like, the tip entire, the keels hardly distinguishable and the pulvinus confined to the adaxial surface (H), so that it has little resemblance to the prophylls of the umbel rays.

The terminal spikelet (t) is, like the lateral, sessile, and is often pushed to one side by the uppermost prophyll. It has one empty scale (R) at the base, presumably an empty glume, an exception to the general statement that there are no empty glumes in *Cyperus*. Similar arrangements, with sharp differentiation of the different kinds of prophyll, have been found in other species of *Cyperus* examined.

Cyperus subumbellatus Kukenth., another common weed of open, well drained places, has rounded stems, and the scales and leaves follow an indeterminate phyllotaxy (fig. 4, I, J). The fragment illustrated, part of a large clump, illustrates the arrangement well. The parent shoot bears leaves labelled arbitrarily a^1 , a^2 , a^3 etc., and of these a^2 , a^3 , and a^4 subtend buds. That in the axil of a^3 is expanded and has burst through its subtending leaf. It bears a two-keeled prophyll p and the leaves 2, 3, 4, etc.

Now it has been claimed by several authors whose work is summarized by Arber (1934), with important additions of her own, that where the prophyll has two keels one is the original midrib of the prophyll and

the other an enlarged lateral. Supposing that the angles between successive leaves remain relatively constant, then following the series 4,3,2,p, down the shoot, the keel x not y appears as the midrib. Blaser (1944) has objected to Arber's suggestion on the grounds that her main criterion for distinguishing the keels was that of size, and 'many of her figures show the largest vein in the wrong keel'. But her claim that not more than one shoot is subtended by a prophyll, and that this shoot springs opposite the keel representing the midrib still stands, and is true of most Cyperaceae.

The prophyll a part of the disseminule

In all Scirpeae and in most Cypereae the glumes fall away from the persistent rachilla of the spikelet to set free the fruits. But in some species of *Cyperus* of the section *Mariscus*, including *C. subumbellatus*, the spikelet falls as a whole. The spikelets are arranged in dense clusters (fig. 4, K), the clusters mostly pedunculate but with a single sessile cluster terminal to the culm. Each individual lateral spikelet has a subtending bract and prophyll at its base (L). On ripening the spikelet falls away taking the prophyll with it, but usually leaving the subtending bract behind. The prophyll is not actually attached to the spikelet, and can be teased away, but clasps the base of the spikelet tightly.

In *Kyllinga*, possibly derived from a *Mariscus* by further concentration of the inflorescence and reduction of the stigmas, the disseminule again falls with the clasping prophyll (Fig. 4, M,N.). In *Lipocarpa* the prophyll may be five-ribbed, but only two of the ribs are of vascular structure (Blaser, 1944) or it may be smooth surfaced without ribs or keel. *Hemicarpha* and *Remirea* are related (Kern, 1962). *Ascolepis* (fig. 4, O,P, *A. capensis* Ridl.) is usually placed in Mapanieae, separated from other genera by the 'chypogynous scales' or 'bracteoles' being 'united' to enclose the otherwise naked flower. But there is no reason to believe that the enclosing structure has resulted from a union, for it occupies the position and has the two keels of the prophyll normally found at the spikelet base in sedges. All these genera may belong to Cypereae, to the group defined by Nees von Essénbach (1835, group I b) as having 'spiculae uniflorae'. Possibly in *Isolepis* also the single median hypogynous scale figured by Clarke (1909) is a prophyll and the genus belongs in Cypereae rather than Scirpeae, a suggestion which follows Pax (1886), who associated it with *Hemicarpha*. This is a rare instance of doubt as to whether or not a particular scale is a prophyll, and so as to how much of the inflorescence constitutes a spikelet.

Geometrical branching in *Kyllinga*

The excellent habit drawing of *Kyllinga erecta* Schum. Thonn. in the Flora of West Tropical Africa shows the straight knotted rhizome with two scales between the origins of successive culms, and my fig. 4, Q, R presents an analysis of a fragment. As in the bulbous variety of *Fuirena umbellata* the scales are a prophyll and a second leaf, and the direction of the phyllotaxy is reversed at each new shoot. Besides the main buds continuing the rhizome from the axils of each second leaf, other buds are found in the axils of the third and fourth leaves of each shoot.

In this *Kyllinga* the internodes of the horizontal parts of the shoots that build the rhizome are well developed, though the internodes at the bases of the culms are short so that the leaf attachments are crowded. In other Cyperaceae with horizontal rhizomes there may be only one internode between successive culms, so that the rhizome bears only prophylls, as in *Eleocharis palustris* (Walters, 1950), or four with a prophyll and three scales as in *Scirpus lacustris* L. (Mora, 1960). In Cyperaceae which spread by long horizontal rhizomes bearing tubers at their ends, each rhizome has a prophyll at its base and an indefinite number of elongated internodes in its horizontal part (Pax, 1886).

Leafy stems in Cyperaceae

Most Cyperaceae have all the stem leaves attached at the base of the culm, but in *Cyperus mundtii* Kunth. there are long horizontal leafy stems, usually half-floating in slowly moving water, clothed throughout with evenly spaced leaves. Still leafy each stem eventually becomes vertical and ends in a short bare culm and inflorescence. Occasional new branches, each with its prophyll (fig. 4, S) spring from the horizontal parts. *Remirea maritima* Aubl. has a similar spreading habit but grows in loose coastal sand. The leaves are reduced to scales on the horizontal parts; on the short vertical parts the leaves are tightly packed, and there is no bare culm between the leaves and inflorescence. These peculiar species are undoubtedly specialised and indicate at least the possibility of a culm becoming leafy. But in other tribes the direction of evolution is less certain, and the habit of the early Cyperaceae cannot be determined.

Prophyll branching in the inflorescence of *Rhynchospora*

Rhynchospora corymbosa Britten (Fig. 5, A-K) grows in the shallow waters of open swamps to about 2 m, usually in pure stand. The long coarse leaves are mostly basal, but others spring from the culm, and there is no gap between these and the inflorescence bract. Each major inflorescence

branch has a delicate tubular prophyll, minutely denticulate on the keels, at its base, hidden in the sheath of the subtending leaf (B).

Whereas in most sedges all the spikelets of a given inflorescence are at about the same stage of development, in this *Rhynchospora* young and fruiting spikelets are mixed (C and D, young spikelets 3, 5 and 7). The culm, once it is developed, continues to bear new spikelets, and may survive the dry season to fruit again later, all with little change in its outward appearance. This is done by prophyll branching. The smaller fragment (E, F) has three successive branches with prophylls a^p , b^p , and c^p , and the larger fragment (C, D) includes the spikelet t terminal to the branch bearing the prophyll t^p , at its base, and four bracts, each of which subtends a shoot, 1, 4, 6 and 8. From the prophylls of these spring 2, 5 and 6 and from the prophyll of 2 shoot 3. Blaser (1944) gives a section of *Rhynchospora inexpansa* Vahl with a similar arrangement.

In the dwarf *Rhynchospora alba* (L.) Vahl (fig. 5, L-T, Irish material) the leaves are distichous and some subtend young shoots. In each shoot the prophyll faces the parent stem, but the new distichy is at right angles to the old. The culm leaves subtend no buds below the inflorescence, whose major branches bear long tubular prophylls (P), reduced to scales in the minor branches (Q, R). Blaser (1944) studied this species and found the smaller prophylls veinless and only slightly keeled, but had no doubt as to their identity.

Tandem branching in *Cladium*

Cladium mariscus R. Br. (Fig. 6, A-H, Irish material) is tall and rough approaching in habit our larger tropical sedges, though of temperate regions. In the inflorescence two branches, major and minor, noted by Mora (1960), spring from each node of the culm (mj , mn), as in *Fuirena*. The prophylls of these branches are not tubular as in most sedges, but are split to the base ventrally, with the edges overlapping. The minor branch is set in tandem ventral to the major, not at its side and not enclosed in its prophyll. The spikelets are crowded (D, E) but their arrangement is normal, each of the lateral spikelets having a bract and prophyll at its base, the terminal spikelet neither.

Loss of prophylls in *Schoenus*

Schoenus nigricans L. (Fig. 6, I-M, Irish material) has long, open, membranous pointed prophylls at the base (I). In the fragment figured the main stem has formed its culm, and this carries leaves a^1 - a^5 . Of these a^3 and a^4 subtend shoots. The prophyll of the younger shoot, b^p , is still entire but that of the older shoot, c^p , is split into two single keeled halves.

The inflorescence is carried on a long bare culm which becomes bracteate near its apex. Groups of spikelets spring from the axils of the larger bracts each spikelet on a distinct pedicel, but without a prophyll (Mora, 1960 and Fig. 6 J). Slight differences of size, position and state of development suggest successive prophyll branching (K), as at the base of *Fimbristylis hispidula* Kunth, b developing from a and giving rise to c and d, but it is difficult to be sure. Near the apex of the inflorescence the bracts are smaller and subtend only one spikelet. As there are no prophylls the terminal and lateral spikelets are similar (L, M).

The spikelet in Rhynchosporae

A terminal spikelet of *Rhynchospora corymbosa* (fig. 5 G) has three empty glumes 1, 2 and 3 at the base, and removal of glume 4 (H) does not expose a flower. But the next glume 5 which hides the lowest flower from view does not subtend it, for the glume and flower lie on opposite sides of the rachilla. In fact this flower is subtended by 4, but is closely enwrapped by the overlapping membranous margins of 5. Similarly removal of 5 does not expose the next flower for it is enwrapped by 6 (I) and there may be yet another flower with no ovary, subtended by 6 and enwrapped by 7, 7 being sterile (J). There is usually only one bisexual flower, the lowest (K), but there may be two.

R. alba has a similar spikelet structure, but with fewer parts (fig. 5, S, T). Clarke's (1909) diagram of *R. wallichiana* and of *Eriospira pilosa* Benth., now transferred from Sclerieae to Rhynchosporae on account of its perianth (Reynal, 1963), agree well. *Cladium* (fig. 6, F-H) has similar enwrapping glumes. Thus in both the terminal spikelet (F, G) and the lateral spikelet (H) glume 3 is wrapped round the lowest flower, which is subtended by 2. In *Schoenus* (L-N) the spikelet has up to five flowers set on a flexuous rachilla, each flower springing from the rachilla above the subtending bract rather than from the actual axil of the bract. Supraaxillary buds are common in Cyperaceae as in the rhizome of *Eleocharis* (Walters, 1950) and the culm base of *Cyperus tenuis* (fig. 4, B).

Pax (1886) described the spikelets of *Asterochaete* and *Elynanthus* as having a structure similar to that of a *Rhynchospora* or *Cladium*. But he showed the bract between the two flowers, corresponding to 6 in fig. 5 J, as a two keeled prophyll. He explained its presence by supposing the lower flower to terminate the main axis of the spikelet, and the second flower to terminate a secondary axis springing from the uppermost bract of the main axis and carrying the supposed prophyll. In *Schoenus* again he and Celakovsky (1887) supposed the spikelet to be a sympodium, each flower above the first terminating a short axis and bearing a prophyll from

which the flower above sprang. The sympodial structure separated Rhynchosporeae from other tribes.

Blaser (1941,b) showed the lower flower of *Rhynchospora macrostachya* Torr. ex A. Gray as terminal, but the disputed bract as having only one vein and no keels. Hamlin's (1955) description of the rachilla of *Schoenus* "carrying the glume above the subtended flower" was clearly based on Pax's theory. Kern (1962) again figured the spikelet of *Schoenus* as a 'rhipidium', but, since he found 'exactly the same' structure in *Cyperus*, believed that here also the spikelet was a rhipidium.

Holtum (1948) pointed out the weakness of Pax's theory. The supposed prophylls of *Asterochaete* and *Elynanthus* had no keels and were in fact glumes, though they might be compressed by the flowers between which they lay and assume angular forms (fig. 5 J, glumes 6 and 7). Again Mora (1960) has described the inflorescence unit of *Cladium* and *Schoenus* as a cymose "Scheinahrchen", identifying the more distal bracts as prophylls subtending the flowers. But his carefully drawn sections show the supposed prophylls to have the same structure as the undisputed bracts, with one keel and one vascular bundle, both median, not two of each. His drawings of a developing unit are also indecisive, for his "sterilen Spelze" appears to subtend the lowest flower and his "Vorblatt 1 and 2 the succeeding flowers of a racemose spikelet. Koyama (1961) appears justified in giving a reduced scirpoid spikelet structure for Rhynchosporeae, and the arrangement of the prophylls, not considered by him, supports this. The peculiarity of the tribe lies in the enwrapping glumes, not in a cymose structure.

Branching in Sclerieae

Scleria naumanniana Boeck. is a loosely tufted perennial, about 1.m high, of dry open bush on laterite or sandy soil (Fig. 7, A-I). The buds at the base have short conical prophylls, soon splitting as the bud bursts through the sheath of the subtending leaf (B). The florets are unisexual, set in spikelets of three kinds, male, female and bisexual (C). Young buds are mixed with the old.

Removal of the subtending bract (D) exposes a series of prophylls, inbricated one within the other (E). Branch 1 carries the prophyll 1^p and several spikelets, removed in D, and 1^p subtends branch 2, and so successively to the youngest shoot 6. As in *Rhynchospora corymbosa*, which has similar prophyll branching, a fruiting culm can survive the dry season and fruit again.

In a bisexual spikelet (F, G) glumes 1 and 2 are sterile, 3 subtends a female flower supported by a three lobed gynophore, but without perianth,

and the remaining glumes take up a subdistichous arrangement, subtending male flowers, of which most have only two stamens. The uppermost glume is small and sterile. The glumes of the male part of the spikelet are pushed aside by the female flower, the more so as the fruit expands.

The female spikelets have only three well developed glumes and the flower appears terminal. But in some spikelets there is a minute, sterile, fourth glume representing the male part of the spikelet (H, I, m).

Scleria verrucosa Willd., a coarse plant of permanent swamps, 1½ m, has a shortly creeping, branched rootstock, with new branches arising where the shoots turn vertically to form the culms (J). The inflorescence branches arise two at each node (K), one from the prophyll of the other, the prophylls, especially that of the minor shoot, being very delicate (L). The spikelets are unisexual, a sessile female usually springing from the prophyll of a pedicelled male spikelet (M, N). The male spikelets have numerous glumes, distichous below but spiralled above, some of the lower and the uppermost sterile, often with one or more glumes (e.g. 5) enwrapping the flowers below (O, P). The female spikelets have three to five glumes, with the flower apparently terminal (Q, R). The lobes of the gynophore enlarge and evert as the fruit ripens.

The male part of the bisexual spikelets of *Scleria* has been interpreted, by Goebel (1888), Mora (1960) and Kern (1962) among others, as a secondary branch arising from a bract of the main axis which carries a terminal female flower. Kern showed an intraspicular prophyll in the position of glume 4 (fig. 7, F, G), marking off the male part. But the dissections of Clarke (1909), Koyama (1961) and Raynal (1963) show no prophyll in this position in the many species they have studied, and Blaser's (1944, b), section of *Scleria reticularis* Michx. shows the scale in question to have a midvein but no keels. In *Hoppia* and in *Diplacrum*, a genus believed closely related to *Scleria*, the sessile male spikelets are subtended by glume-like scales below the female spikelet, but they are set off by keeled prophylls leaving no doubt as to their spicular nature. Indeed in all *Sclerieae* the prophyll arrangement is a safe guide to spicular identity.

It might be difficult, in the absence of any remnant of the male part of the spikelet, to say whether the female flower was lateral or terminal. But since in bisexual spikelets it is always lateral, it is presumably so in all species of *Scleria*, and probably in all species of *Cyperaceae*, even when it appears terminal. The lobes of the gynophore in this and other *Sclerieae* have been interpreted as perianth segments. But Blaser's (1941, b) sections show vascular bundles on their way to the ovary deviated into the lobes, not ending in them as they would if they were perianth segments.

In most Cyperaceae the region of the culm between the bud-subtending basal leaves and the bracts of the inflorescence bears no buds and is unbranched (Mora, 1960), and even if the culm is leafy as in *Fuirena* or *Rhynchospora* the culm leaves subtend no buds. But in *Scleria naumanniana* buds are found in the axils of the culm leaves, though they seldom develop unless the culm is cut. In *Scleria barteri* Boeck. the culms are profusely branched and scramble over bushes to 5m., clinging by the retrorse spicules of the stems and leaves. As in *Cyperus mundtii* this branching is clearly a secondary, not a primitive, feature of the group, as it appears to be in Cyperaceae as a whole.

Mapanieae

Mapanieae are mostly large tropical plants with wide leaves. Their basal parts resemble those of other tribes. *Hypolytrum* sp., nr. *heterophyllum* Boeck, (fig. 8, A), growing in rich damp places in semi-shade, has wide basal leaves with spreading scaly stolons (B) breaking through their attachments. The prophylls of these stolons are short and conical, resembling those of a *Cyperus* or *Scleria*. But in the inflorescence the branching is peculiar. Rüter (1918), quoted by Blaser (1944), showed the prophyll in *Scirpodendron* and *Mapania* more or less divided into two separate bracts, each having a single keel and each subtending a shoot (C). In *Hypolytrum* the main branches again come off three together, the group as a whole subtended by a large bract, but each branch has its own prophyll (D). The minor lateral branches carrying heads of spikelets have small tubular prophylls at the base (E). Kern (1962) has noted that, as in other Cyperaceae, the terminal head in Mapanieae has no prophyll near its base. Each bract of the head subtends a reduced spikelet enwrapped by a pair of ciliate keeled scales, united below and subtending a pair of stamens (F) with a naked female flower between (G). This is the most reduced form of spikelet found in Mapanieae, for other genera have unkeeled scales, often joined to a tube, with or without single stamens in their axils, set between the keeled pair and the female flower (H), richly developed in *Chorisandra* (I) and *Scirpodendron*.

The keeled scales appear to be derived from a single prophyll subtending two flowers, each reduced to a single stamen. They are found throughout the tribe except in *Chrysithrix*, where, as in *Eleocharis* the spikelet is solitary and terminal to the culm (Clarke, 1909), so that there could be no prophyll at its base. In general the structure is uniform and, contrary to Kern's (1962) proposal, it seems reasonable to retain the *Scirpodendron* group and the *Scirpus* group at subfamily level.

Bentham (1877) believed that the peculiar spikelet was in fact a single floret with numerous perianth segments and stamens, but Goebel (1888),

after detailed consideration, set this suggestion aside. Indeed Bentham's proposal did not explain the frequent presence of scales within the outer stamens. But in the reduced form seen in some species of *Mapania* the spikelet may resemble a single floret of a *Scirpus*, particularly *S. membranaceus* Thunb. which has a pair of keeled scales, and on such a comparison the modern synanthial theory of Holttum (1948), Koyama (1961) and Kern (1962) is based. The complex spikelet of unisexual florets of such general as *Scirpodendron* is supposed to have been reduced to a simpler type resembling that in *Mapania*, and so to the floret of a *Scirpus*. The florets became re-arranged in new spikelets of a higher order, and from Scripaeae other tribes were derived.

Evidence from the prophylls, so far as they are known, does not favour the synanthial theory. The scirpoid type of single prophyll subtending only one bud, if any, opposite one of the keels can be matched in many families of monocotyledons, so it is likely to be primitive for Cyperaceae, while the divided type of prophyll subtending two buds is restricted to Mapanieae, and appears to be a specialization. Possibly *Scirpus membranaceus* should be transferred to the Mapanieae which it resembles in general habit and massive inflorescence, as well as in spikelet structure (Compare Clarke's 1909 figure with my fig. 9 F).

Reductions of the florets by loss of perianth, stamens or ovary occur in other tribes of Cyperaceae where they are always regarded as specializations, and a solitary, apparently terminal ovary is found in some species of *Scleria*. A monograph giving the general structure of Mapanieae with plans of the branching is still needed (Kunth in 1837 wrote of them "structura mihi adhuc obscura"), but the little we know favours an evolution from *Scirpus* to *Scirpodendron* (J-L) rather than the reverse.

Note on Cariceae

The Cariceae are, on the whole, an extratropical group, but are well represented on the mountains of East Africa. Fully discussed by Schultze-Motel (1959), Koyama (1961), Kern (1962) and Raynal (1963), with references to earlier work, they are unique in the placing of the solitary female flower in the axil of a utricle, a modified prophyll at the base of a spikelet, and not of a glume. How the flower reached that position is unknown, but there is no need to follow Gilley (1952) in his proposal for a new family, Kobresiaceae, for in Mapanieae also the prophyll is fertile, though it subtends two male flowers, not one female.

Hamlin (1955) says that authorities generally look to the Rhynchosporae for the 'progenitors' of the tribe, but they may come from Sclerieae in which the flowers were already unisexual and without a perianth.

Bentham (1877) actually placed *Kobresia* in *Sclerieae* and *Schoenoxiphum rufum* Nees as figured by Clarke (1909), resembles *Scleria naumanniana*. The point cannot be determined on spikelet structure alone, but anatomical or embryological studies might settle the matter.

Nature of the prophyll

Blaser (1944) believed the cyperaceous prophyll to be 'merely a leaf', 'occasionally distinguishable by position and modifiable in various ways', and Koyama (1961) suggested an origin within the Cyperaceae from a 'metamorphosed bract scale' which 'would have become empty by the abortion of its axillary flower secondarily'. The 'occasionally' seems weak, for there is seldom any difficulty in making the distinction. Koyama's further statement that prophylls are homologous within genera also seems too limited, for they seem homologous throughout and even beyond, the family. Their very rare absence, as in the inflorescences of *Schoenus* (fig. 6, J) and *Chrysithrix* (fig. 7, D) is at once apparent. Nor does their presence 'differentiate rachillae from branches' for prophylls are found at the bases of both, and only at the bases of the florets are they absent.

Origin and development of Cyperaceae

Ziegenspeck (1963), Schultze-Motel (1959) and Takhtajan (1959) have summed up the evidence for the classical conception of an origin of Cyperaceae from Liliiflorae, probably through Juncaceae, evidence based on the structure of the plant, pollen and embryo, with adequate references. But Kern (1962) found a derivation 'from Liliiflorae, especially Juncaceae, impossible'. If the scirpoid type of spikelet is the most primitive in Cyperaceae it is certainly not impossible, and fig. 9 suggests how it may have happened. Wind pollination, with reduction of the flowers and their grouping in clusters are characteristics of Juncaceae. The arrangement of the bracts, prophylls, branches of different orders and lengths, and sessile terminal and stalked lateral flower clusters in *Juncus lamprocarpus*, Ehr., and the loss of prophylls within the clusters in *Luzula campestris* DC. (Buchanau, 1866) precisely parallel the inflorescence structure of typical Scirpeae. Further reduction of the perianth, association of the florets in spikelets and reduction of the ovules to one would then lead to a form of the *Scripus sylvaticus* habit. From this other Cyperaceae could have evolved, including the paniculate *Desmoschoenus*, chosen by Koyama (1958) as closest to the prototype of *Scripus*. The only form difficult to derive in this way is *Oreobolus*, where the flowers are not arranged in spikelets. Possibly this comes, by reduction of the ovules to one, from a juncaceous plant similar to *Distichea*, but with bisexual flowers. It should, in this case, be removed from the Cyperaceae.

Primitive features would then be, as Tutin (1954) stated, leafy stems, spikelets of many bisexual florets spirally arranged with few or no sterile glumes, each flower with a perianth, three stamens and three stigmas, and the ovary ripening to a trigonous nut not enclosed by a perigon or closely enfolded glume. The leafy stem is somewhat doubtful, but there may be added the presence of a prophyll at the base of all branches down to spikelet level and the absence of branching from the axils of these prophylls.

Classification could follow orthodox lines without the changes in order implied by the synanthial theory, returning to Clarke's system as modified by Marloth in the Flora of South Africa (1915), given by Koyama (1961), only substituting Rhynchosporae for the less familiar Schoeneae:

1. Scirpeae (Primitive Cyperaceae)
2. Cypereae (From Scirpeae. Glumes distichous, perianth lost)
3. Rhynchosporae (From Scirpeae. Flowers usually few, each often enwrapped by the glume above).
4. Mapanieae (Possibly from Rhynchosporae. Prophylls of spikelets more or less split and subtending two male flowers, usually with further monandrous male flowers below the solitary female floret, perianth lost).
5. Sclerieae, including Lagenocarpeae (From Rhynchosporae. Flowers unisexual, the female solitary, the male above the female or in separate spikelets, perianth lost).
6. Cariceae (Possibly from Sclerieae, Prophylls of spikelets often forming utricles, subtending one female flower, with male florets above or in separate spikelets.)

Tropical Cyperaceae

Corner (1954), developing his 'durian theory', suggested that many extra-tropical plants were the dwarfed and secondarily simplified descendants of larger and more primitive types of tropical forests, where many of these forms still lived. Holttum (1948) and Kern (1962) believed that a study of tropical Cyperaceae might throw light on the origin of the family. But near Lagos and Kampala few Cyperaceae grow in dense forest, in contrast to the many specialized forest Gramineae, mostly Paniceae with broad leaves and green stilt roots. Only *Cyperus maculatus* Boeck. and *C. soyauxii* Boeck. are restricted to shade, and these are not specially remarkable species. Some larger species of *Scleria*, *S. racemosa* Poir. and *verrucosa* Willd. and the large *Cyperus renschii* Boeck. and

fischerianus Schimp. ex Hochst. grow in forest, but along streamsides where there is some break in the canopy, and they also grow vigorously where it is damp but there are few trees. *Fuirena* is tolerant of light shade, but grows better in the open and only on ground which is damp for at least part of the year. *Scleria naumanniana* is a plant of dry bush, but only where the bush is open, usually from human interference. Even the climbing *Scleria barteri* is confined to low secondary bush and is not found in tall forest.

In fact most of our Cyperaceae are plants of open damp places, particularly shallow swamps rather than of shady or dry situations. Their abundance depends on destruction of forest or unsuitability of the habitat for forest growth, and they have undoubtedly been spread by human habitation, cultivation and burning. Many are found in the precincts of towns. Some Mapanieae do grow in damp forest conditions, but their morphology appears peculiar and they seem to represent an end product of evolutionary specialization. Cyperaceae appear to have invaded the forest from more open situations rather than the reverse.

Even if the essentials of the durian theory were accepted this would not imply the primitiveness of tropical forms. For, as Corner (1954) pointed out, Juncaceae are mainly 'leptocaul and extra-tropical', though possibly derived from a pachycaul such as *Prionia*. (There are no Juncaceae in the forests and savannahs of Nigeria proper or lowland Uganda, but they grow on the highlands of East Africa and the Cameroons.) If then Cyperaceae are derived from Juncaceae the transition probably occurred outside the rain-forest.

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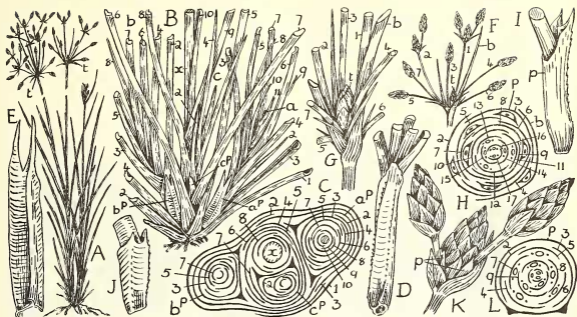


Fig. 1 *Fimbristylis*:

A — *F. dichotoma*, habit. B — *F. obtusifolia* portion of base. C — plan of B. D — young tubular prophyll. E — old, split prophyll. F — *F. dichotoma*, inflorescence. G — central part of F. H — plan of F. I — prophyll of larger branch. J — prophyll of smaller branch. K — cluster of spikelets. L — plan of lateral spikelet.

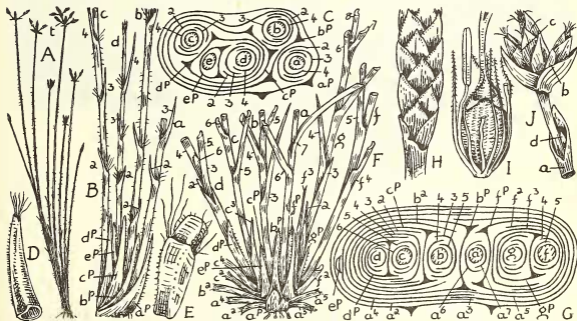


Fig. 2 *Fimbristylis*, *Eleocharis*, *Scirpus*:

A — *F. hispida*, habit. B — portion of base. C — plan of B. D — prophyll from base. E — prophyll from inflorescence. F — *F. dichotoma*, portion of base. G — plan of F. H — *E. mutata*, base of spikelet. I — flower. J — *S. brachyceras*, cluster of spikelets.

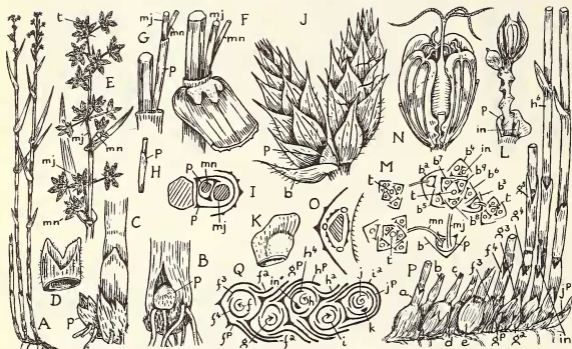


Fig. 3. *Fuirena umbellata*:
 A — habit. B and C — base of culm. D — prophyll from base. E —
 inflorescence. F — branches from culm. G and H — bases of branches.
 I — plan of F. J — pair of spikelets. K — prophyll from base of spikelet.
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 N — flower. O — plan of flower. P — bulbous from. Q — plan of P.

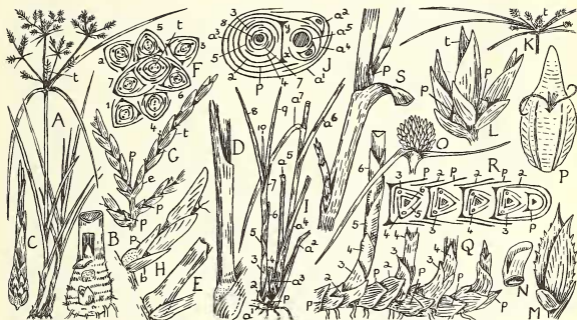


Fig. 4. CYPEREAE. *Cyperus*, *Kyllinga*, *Ascolepis*.
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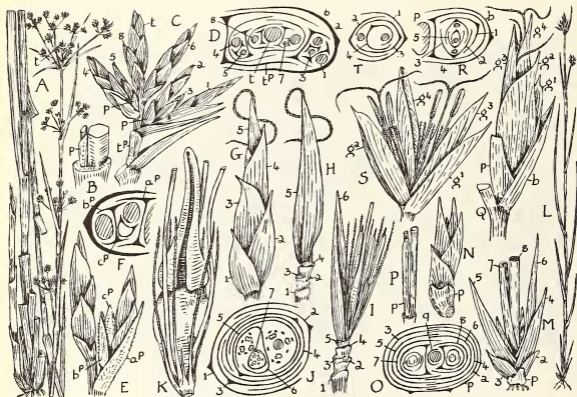


Fig. 5. *Rhynchospora*:

A — *R. corymbosa*, habit. B — inflorescence branch. C — group of spikelets. D — plan of C. E — prophyll branching. F — plan of E. G — spikelet. H — spikelet, four glumes removed. I — spikelet, flower exposed. J — plan of G. K — ripe fruit. L — *R. alba*, habit. M — base of plant. N — young shoot. O — plan of M. P — inflorescence branch. Q — spikelet. R — plan of Q. S — terminal spikelet spread. T — plan of S.

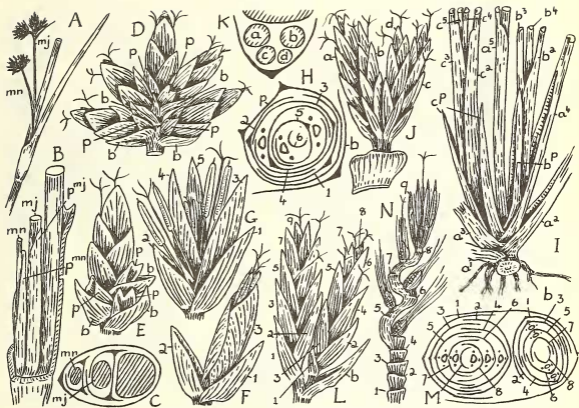


Fig. 6. RHYNCHOSPORALES: *Cladium*, *Schoenus*.

A — *C. mariscus*, inflorescence fragment. B — branch bases. C — plan of B. D — cluster of spikelets. E — terminal spikelet and bases of three others. F — Third, unwrapping glume. G — spikelet spread. H — plan of G. I — *S. nigricans*, base of plant. J — group of spikelets. K — plan of J. L — two spikelets. M — plan of L. N — rachilla and florets.

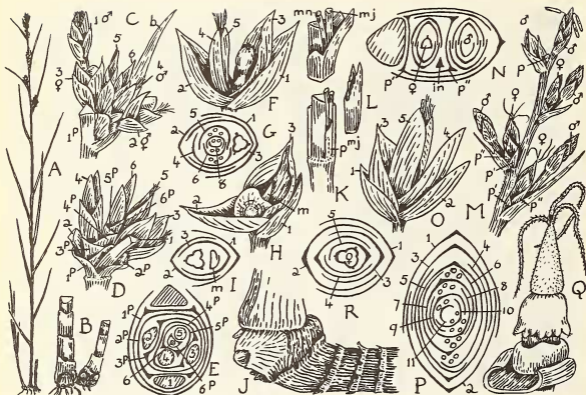


Fig. 7. *Scleria*:
 A — *S. naumanniana*, habit. B — bases of culms. C — cluster of spikelets.
 D — prophyll branching. E — plan of D. F — bisexual spikelet, spread.
 G — plan of F. H — female spikelet, fruit fallen. I — plan of H. J —
S. verrucosa, base of culm. K — inflorescence branching. L — prophyll
 from K. M — fragment of inflorescence. N — plan of spikelet group. O
 — male spikelet, spread to fifth glume. P — plan of O. Q — female flower.

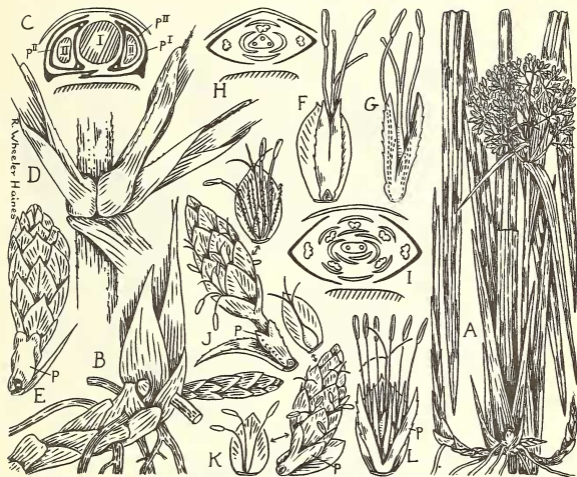


Fig. 8. MAPANIEAE:

A — *Hypolytrum heterophyllum*, habit. B — base of plant. C — *Mapania*, inflorescence branches, after Rüter (1918) and Blaser (1944). D — *Hypolytrum*, inflorescence branches. E — Head with prophyll. F — Bract with spikelet. G — spikelet, dorsal view. H — *Thoracostachyum* after Clarke (1909). I — *Chorizanthe* after Clarke (1909). J — scleroid bract and spikelet. K — reduced spikelet with unisexual flowers. L — Mapanoid spikelet.

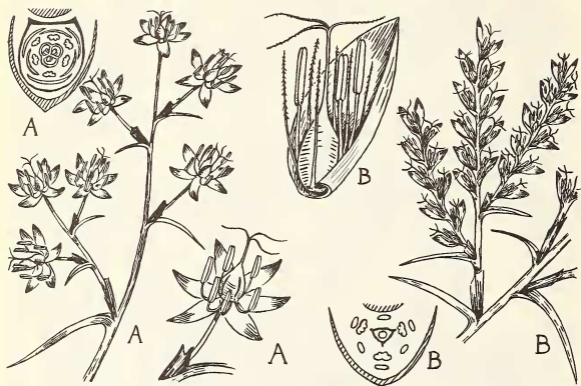


Fig. 9. Origin of Cyperaceae, orthodox theory:
 A — Liliiflorous plant, with single flower and plan. B — primitive
 scirpoid plant with flower and plan.